

Foraging Success of Neotropical Robber Flies: Variation with Attack Distance and Angle

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Adults of most robber fly species are sit-and-wait predators that attempt aerial capture of flying insect prey. Attack flights are discrete, easily observed actions, and previous investigators (e.g., Dennis and Lavigne, 1975; Scarbrough and Norden, 1977; Shelly, 1984a) have estimated rates, distances, and success probabilities of attack flights for a variety of asilid species. Success probability (or more commonly capture efficiency) has usually been expressed as the proportion of all attack flights that result in prey capture (e.g., Scarbrough, 1978; Lavigne, 1982; Shelly, 1984b). Although this measure conveniently provides a single estimate for a species, it ignores possible variation in success probability among attack flights of varying distance and angle. Several studies (Scarbrough, 1978, 1981, 1982; Scarbrough and Sraver, 1979; Lavigne et al., 1983) have reported that most prey captures result from relatively short attack flights. However, this finding provides no information regarding the relationship between success probability and attack distance, since no data are given regarding the frequencies of attack flights of differing distances. While conducting a comparative study of asilid foraging behavior (Shelly, 1984a), I obtained visual estimates of the distances and angles for both successful and unsuccessful attack flights for two closely related species at the study site. Here I compare success probabilities among attack flights of varying distance and angle.

Data were collected during May–August 1979–1981, within the moist evergreen forest of Barro Colorado Island (BCI), Panama. Complete geologic, climatic, and floristic descriptions of BCI are given in Croat (1978) and Leigh et al. (1982). On BCI, *Oidardis* sp. and *Eumecosoma gibbum* [Fisher (unpubl.) suggests that this species actually belongs in the genus *Oidardis* and was incorrectly placed in *Eumecosoma*] perch in deep shade on twig tips between 0.5–0.75 m above ground (Shelly, 1985a, 1985b). Mean wet weight and body length for a sample of 5 ♂ and 5 ♀ were 4.2 mg and 4.8 mm for *Oidardis* sp. and 9.4 mg and 6.1 mm for *E. gibbum*. Individuals of both species feed primarily on nematocerous Diptera and Coleoptera; these taxa made up 71% of the diets for both species (Shelly, 1985a, 1985b). Prey were usually <4 mm in body length, and 85% and 57% of the prey were between 0.5–2.0 mm for *Oidardis* sp. and *E. gibbum*, respectively (Shelly, 1985a, 1985b).

Observations were made between 1000–1500 hr and were recorded on tape for later transcription. Observations were made during sunny conditions, and light levels (measured with a cadmium-sulphide photographic light meter, Shelly, 1984a) within the shaded understory were usually between 150–500 lux. Individuals were observed for 15 min unless lost from view prior to that time. Individuals were

Table 1. Success probabilities (% successful attacks) for attack flights of varying angle and distance. Values in parentheses represent sample sizes for the different combinations of angle and distance.

Angle	Distance (cm)			
	1-15	16-30	31-45	>45
>45° AH	42.4 (33)	33.3 (27)	20.0 (10)	10.0 (10)
1-45° AH	46.1 (78)	34.0 (50)	22.3 (22)	15.4 (13)
1-45° BH	47.8 (69)	38.6 (57)	19.0 (21)	14.3 (14)
>45° BH	18.7 (32)	9.5 (21)	0.0 (8)	0.0 (8)

quite easy to approach, and observations were generally made from a distance of 0.75–1.0 m. Field determination of sex was difficult, and consequently the sex of individuals observed was unknown.

Data are presented only for those attack flights for which I obtained estimates of both distance and angle and actually saw the prey item that elicited the attack. Distances were assigned to intervals of 15 cm, and angles were categorized as >45° above horizontal (hereafter AH), 1–45° AH, 1–45° below horizontal (hereafter BH), and >45° BH. The few attack flights judged to be perfectly horizontal were omitted from analysis. Although restricting analysis to attacks with “known” targets greatly reduced sample sizes (since prey were small and often difficult to see), it also eliminated the possibility of including flights made in response to movement of “non-prey” items, e.g., birds, falling or swaying leaves, or sun flecks. To increase sample sizes, data from *Oidardis* sp. and *E. gibbum* were pooled. This computational procedure was considered justified given the species’ similarity in perching site, dietary composition, and foraging behavior. Since data regarding rates of attack and relocation flights were being collected simultaneously as part of the comparative study (Shelly, 1984a), I did not disrupt normal foraging activity through collection of captured prey (which are affixed to the proboscis of a feeding asilid). As a result, I could not assess the possibility that attack flights of differing distances or angles resulted in the capture of differing sizes or types of prey (see Scarbrough, 1978, 1981). Within angle and distance categories, heterogeneity among success probabilities was tested using a G-test (Sokal and Rohlf, 1969:575).

Success probabilities varied significantly with attack distance for attacks between 1–45° AH and 1–45° BH ($P < 0.01$ in both cases; Table 1). In these categories, success probabilities decreased from 34%–48% for attacks <30 cm to approximately 15% for attacks >45 cm. Data for attacks >45° AH display a similar trend, and the lack of a statistically significant effect ($P < 0.20$) probably reflects inadequate sample sizes. Although small sample sizes may have precluded detection of a significant distance effect for attacks >45° BH as well, the available data suggest that such an effect may be much less pronounced for these attacks. Capture probabilities for attacks >45° BH ranged only between 0–19% among the 4 distance intervals.

Success probability was dependent upon attack angle for flights of 1–15 cm and 16–30 cm ($P < 0.05$ in both cases; Table 1). For these intervals, success probabilities were similar among attacks >45° AH, 1–45° AH, and 1–45° BH, and these probabilities were in turn much greater than those noted for attacks >45° BH.

Among flights of 1–15 cm, for example, the capture probability of attacks $>45^\circ$ BH was only 19% compared to values of 42%–48% among the 3 other angle intervals. By comparison, success probabilities for attacks >45 cm varied only between 0–15% among all angle intervals.

I interpret these data in the following manner. The trend for capture probabilities to decrease with increasing attack distance probably reflects a combination of two factors. First, more distant prey may be more likely to detect and successfully evade an attack than prey flying close to a perching asilid. In addition, an asilid's ability to accurately assess the suitability of a potential prey (in terms of its palatability, hardness, defensive armature etc.) may decrease with increasing distance to the prey. As a result, a greater proportion of longer attack flights may not involve an attempted capture at all but result only in an investigation (a "closer look") of the potential prey. Given the short duration (<1 –2 sec) of most attack flights, however, it was not possible to distinguish between "active" prey escape and "investigation only" in accounting for unsuccessful attack flights.

Regarding attack angle, several workers (Melin, 1923; Lavigne, 1970, 1971; Hespenheide, 1978; Scarbrough, 1982) have speculated that attack flights of asilids are more likely to be successful if prey are well back-lighted, i.e., distinctly silhouetted against the sky. Perhaps, then, the species were less able to accurately perceive and track prey flying beneath them, since the background was a mixture of very dark shades (e.g., fallen leaves, mud etc.). If so, both the potential for prey escape and the aforementioned tendency for investigation flights may have been greater for steep, downward attacks. The similarity of capture probabilities among attacks >45 cm suggests that differences in back-lighting have less effect upon prey capture among these longer flights.

ACKNOWLEDGMENTS

I thank E. Fisher for much taxonomic assistance and W. Weaver for valuable discussion.

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